MIGRATORY ORIENTATION OF AMBYSTOMA MACULATUM: MOVEMENTS NEAR BREEDING PONDS AND DISPLACEMENTS OF MIGRATING INDIVIDUALS

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Migrating spotted salamanders, *Ambystoma maculatum,* tend to enter and leave breeding ponds near the same point (Shoop, 1965). This paper confirms the original observation and presents results of observations and experiments designed to further elucidate the problems of migratory orientation of spotted salamanders.

METHODS

Animals from two breeding ponds (A and B) in Wellesley, Massachusetts were studied from 1964 to 1967. Nylon-coated, screen fences 40 cm. high, buried 15 cm. in the soil, surrounded the ponds; deep can traps were buried at intervals along both sides of the fences. Other fences from 10 to 200 m. long with traps along both sides were located at varying distances (15 to 175 m.) from the fence surrounding Pond A. Details concerning Pond A and methods are described by Shoop (1965); Pond B is in mixed hardwood-pine forest adjacent to a golf course.

Traps were checked regularly throughout the day and night during the breeding season and at dawn during the rest of the year except when snow covered the traps. The trapping method exposed the animals to increased predation by raccoons; several salamanders were killed before a wire with electrical charger was added around the outer face of the fencing about 15 cm. above the ground. Some animals were released on the Wellesley College campus in a 40-m.-diameter arena with traps along the inner face of a 0.5-m.-high surrounding fence. All animals were individually marked by toe-clipping. Statistical procedures follow Batschelet (1965).

CONFIRMATION OF EARLIER OBSERVATIONS

The relation between point of entry and exit of Pond A by animals during 1964, 1965, and 1966 and mean vector values, 99% confidence intervals for mean vectors, and angular deviations are presented in Figure 1. In all cases corrections for trap intervals are included in the vector determination. The r values vary from 0.42 to 0.55, indicating some dispersion but non-random distribution. In all three cases the mean exit vector falls within the consistent direction (Shoop, 1965) in relation to the point of entry into the pond, and the 99% confidence intervals for the mean vectors overlap. The data for the three years are not
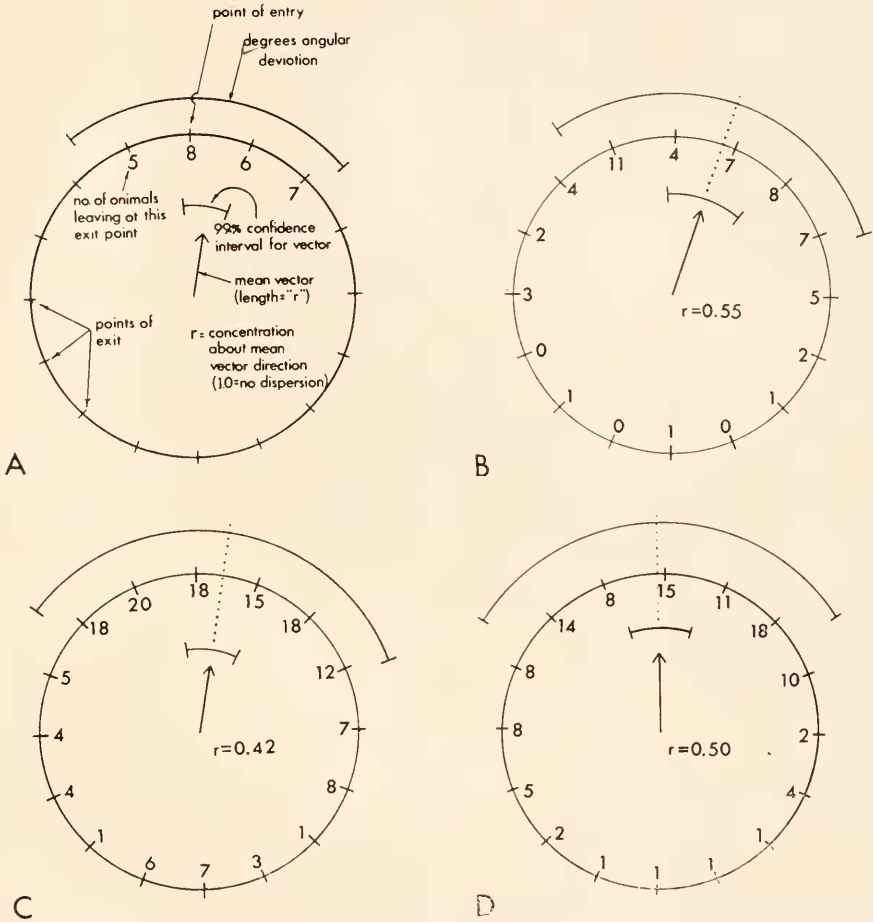
FIGURE 1. Relation of exit point at breeding pond border to point of entrance (top of circle is point of entry, not necessarily north): A, explanation; B, 1964; C, 1965; D, 1966. The 99% confidence intervals of the mean vectors overlap indicating highly significant correlation between years.

significantly different. Animals collected only at entry or exit, or animals used for displacement studies in 1966 were not included in the vector determination.

When interpreting the data of movements into and out of the breeding pond, certain aspects of the experimental design should be considered. The pond was circular with a steep bank, a rather uncommon type of vernal pond. This allowed for close placement of the surrounding fence with traps at the sixteen compass points, and since all recorded directions are in relation to the center of the pond, the data may be more refined than is biologically significant. In reality, a migrating salamander may not move toward the center of the pond but merely attempt to intercept the border. An animal moving from a point east (90°) of the pond center may intercept the border anywhere from 0° to 180° and therefore have a
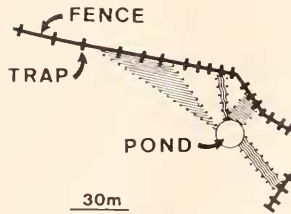
FIGURE 2. Corridors of travel of 4 animals (1967) selected to avoid overlap and show range of variability (N = 36). One-half distance to next trap included in corridors. The fences and traps border forest areas.

"successful" migration. Conversely, the animals may leave the pond anywhere between 0° and 180° and be on the east side of the pond. Considering the amount of dispersion, this type of orientation may actually be more typical of the biologic situation. That a statistically significant number of animals did choose consistent headings in relation to the point they entered the pond indicates that the animals tend to use the same track even though their terrestrial retreats may not be closest to the entry point. Additionally, animals determined as taking "poor" headings may correct for their "error" after leaving the pond.

Studies utilizing fences at varying distances from breeding ponds in 1966 and 1967 seem to confirm the above suppositions. When migrating in a meadow to and from the pond many animals tend to limit their movements when within 100 m. of the pond to a narrow corridor 10 to 30 m. wide. Some corridors used by the salamanders in 1967 are represented in Figure 2. In 1967 36 animals were caught at the forest border and pond border at entry and exit (4 captures each). The corridor used in crossing the meadow to and from the pond may have little relation to the movement of an animal in the forest. Figure 3 shows capture points of an animal moving in an easterly-westerly corridor at a great angle to a line drawn between capture points at the forest border and in the forest. Time between the last two captures was 6 days.

Of the animals collected in successive years, most seem to travel in the same corridor to and from the pond (Fig. 4), although some apparently use different corridors. A pattern of different corridors for entry and exit (seen in 3 animals) may be repated in successive years (Fig. 5A). A few animals seem to move in no definite pattern (Fig. 5B).

FIGURE 3. Movements of a single individual, 1967. ● = capture point; → = direction of movement; . . . . = shortest distance between capture points.
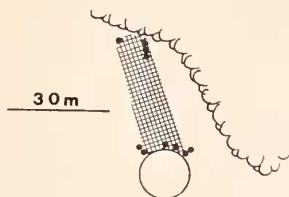
FIGURE 4. Capture points of a single individual, 1965–67. Dots around pond represent captures on entry and exit, 1965–67. Dots at forest border, entry and exit points 1966–67. Shaded area is probable corridor of travel.

EXPERIMENTS INVOLVING DISPLACEMENT OF MIGRATING SALAMANDERS

Displacements in the field

Since migrating animals tend to use the same track into and out of a breeding pond, they may possess an ability to utilize a directional tendency (Griffin, 1952, "Type II orientation," or Schmidt-Koenig, 1965, "compass orientation"); if familiar landmarks or local sensory cues are unavailable or not utilized, they may move in a prescribed direction or its reciprocal (along a directional axis). Assuming that only a compass sense is involved, the animals should fail to reach the pond in the following situation: animals are captured at the pond border, carried 90° around the pond, and then taken in a straight line away from the pond and released at a location where familiar landmarks are obscured. For example, if an animal that had migrated from a terrestrial retreat east of the pond to the east border of the pond, was moved to a point north of the pond, it would travel east or west and miss the pond. The following experiments tested this possibility.

Twelve animals captured at night in the ENE trap at Pond A border were placed in opaque containers and transported at dawn to four locations. Three animals were released 20 m. from ENE; three at 135 m. from ENE; three at 45 m. from NNW; and three at 175 m. from NNW. Of six animals collected in trap NNW, three were released 20 m. from ENE and three 45 m. from NNW. Results of this experiment are presented in Table I. One animal released 135 m. from ENE was killed by raccoons on return to the pond fence.
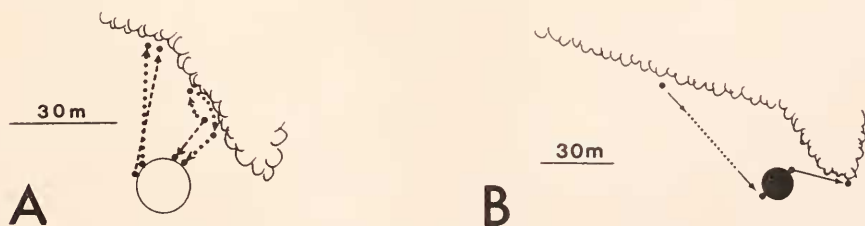

FIGURE 5. A, Movements of a single individual, 1966 (dashed line), 1967 (dotted line). Looping movements (1967) due to dry weather with animal returning to forest. Note different exit and entry corridors. B, Movements of an individual showing no regular pattern, 1967.

One of three males caught at the pond border in trap NNW and transported to a point in a meadow 45 m. NNW of this trap behaved unexpectedly when released under cloudy skies and a NW wind (*ca.* 10 knots). Instead of crawling under cover as animals released in daylight usually do, the salamander, out of sight of the pond or its bordering trees, extended its limbs and slowly moved its head from side to side. Within a few seconds it began to move uphill at a heading of 153°. After moving approximately 3 m. in a straight line, it stopped, repeated the limb extension and lateral head movements, changed its heading to 170° and continued this heading with occasional pauses, moving over the ridge and down to trees bordering the pond where it burrowed under leaves west of the pond center. Slight detours around obstructions were made, but the resulting path of travel on the 34 m., 170° route varied less than 1 m. from a straight line. This animal paused nine times during the 27-minute excursion with a rate of travel during the active portions of about 2 m. per minute.

Except for animals released 20 m. from ENE, all the returning animals had to move some distance uphill before reaching the pond. Animals released 175 m. from NNW were in a different drainage system and had to cross a 9-m.-high

TABLE I

Results of releases of animals originally captured at pond border

Point of capture at pond	Point and direction of release	Returns to pond no. released
ENE	20 m. ENE	3/3
ENE	45 m. NNW	3/3
ENE	135 m. ENE	2/3
ENE	175 m. NNW	3/3
NNW	20 m. ENE	2/3
NNW	45 m. NNW	3/3

ridge with 35° slopes. The time required to return to the pond varied from two to ten days but extremely dry weather also slowed normal migration of other animals at this time. One of the two animals not reaching the pond returned the following year.

In a related experiment late in the 1966 breeding season, 57 animals moving from many directions and collected on arrival at another pond (B) were released at points 200 and 250 m. from Pond B. A salamander returning from the 200 m. release point could encounter any of three other ponds never known to harbor breeding salamanders; return from the 250 m. release point involved crossing a lawn, a large, steep (35° slope) 25-m.-high ridge, and possibly encountering a permanent pond. Two days after the releases the area between the pond and the release points burned, adding strong odors to the area.

Of 28 animals released 200 m. from the pond, 13 were eventually recaptured at the pond border, 7 in the same season, 6 more one year later. Nine of 29 released at 250 m. were eventually recaptured at the pond border, one the same season, one in the autumn, and 7 the following spring. Returns of the same season tended to enter the pond at points nearest the release point. In

both cases returns after two years approximated the percentages of returns by non-displaced animals.

Since the ability of some animals to return from distances up to 250 m. was established, four animals (two males, two females) were collected at dawn at Pond B border early in the 1967 breeding season, placed in covered containers and carried in a truck for one day. At night, phosphorescent vinyl bands were placed around the bodies of the animals, and they were released on a golf course fairway during a heavy rain, 500 m. from Pond B. Return to the pond involved crossing over 100 m. of lawn, encountering up to four temporary ponds, one road, and a small stream.

At release all four animals took headings within 15° of the pond direction. They were turned around by hand but they immediately headed in the pond direction (uphill) and moved approximately 25 m. before being lost from view. After 11 days one of the animals (♀) arrived at the pond border trap nearest the release site. The other three animals were not seen again.

If orientation to a breeding pond is a simple geotaxis, rheotaxis or random search, some migrating animals collected while moving to a breeding pond and displaced close to another breeding pond should then move into the "new" pond. Negative results would suggest that geotaxis, rheotaxis, or random search must be coupled with unknown qualitative factors of the pond itself or that these taxes are not the major factors used in finding the pond.

To test for the above taxes, nine salamanders captured as they moved to Pond B were carried at night in covered containers to sites near Pond A. Three animals were released in a short-grass meadow at each of three compass points (0°, 90°, and 270°) 10 m. from the Pond A border. In two cases, the pond was downhill from the release site; in the other, slightly uphill. None of the animals (6 males, 3 females) moved to the new pond (A). Eight of nine control animals (captured at the Pond A border) moved to Pond A. The following year three of the displaced animals (all males) were recaptured at Pond A, and two of these animals were seen the succeeding year.

Six males transported from the Pond B border and released in the center of Pond A stayed within Pond A from four to 22 days. Their exit directions bore no relationship to the directions from which they attempted to enter their original pond (B) or the direction to Pond B. One of these animals returned to Pond A the following year and was captured while migrating in a nearby wooded area the succeeding year but not at the Pond A border.

Displacements to an arena

In an effort to remove all possible local cues surrounding breeding Pond B, 106 migrating animals were transported to the laboratory and maintained in running lake water aquaria for periods varying from three to eight days. These animals were released one or more times in a 40-m.-diameter arena on the Wellesley College campus under cloudy and clear skies at night during the normal migration period. No significant differences in performances between males and females or between cloudy and clear conditions were noted. A total of 547 releases was made, and the capture points around the inner face of the fence were determined.
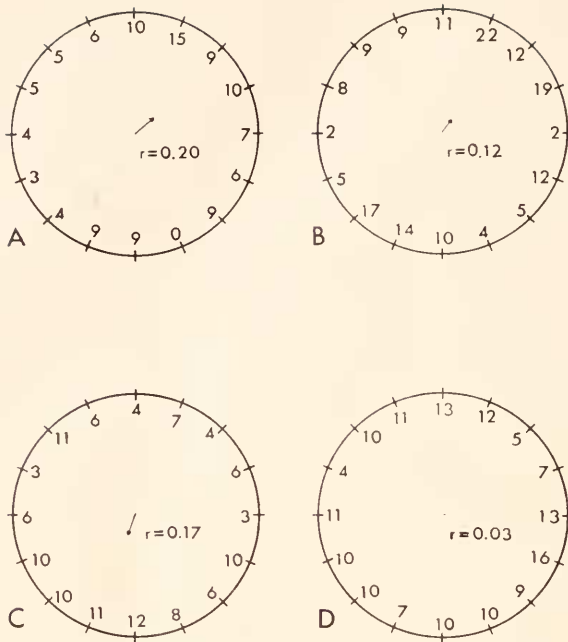
FIGURE 6. Representation of capture points of animals released in arena about one mile from home pond. A, Relation of headings of animals released facing 90° to the left of their heading when captured in the field; top of circle represents original heading in field, not north. B, Headings of animals released by removal of covering container, in relation to original heading in field; top of circle represents original heading. C, Compass headings of animals released facing ENE; top of circle is N, SSE is direction to home. D, Compass headings of animals released by removal of covering container; top of circle is N, SSE is direction to home.

The data obtained by releasing animals facing 90° to the left of their original heading in the field, or released at chance headings (by removing a covering container), in relation to direction of original field heading are random ($r \leqslant 0.20$; Fig. 6 A, B). Pooled results of releases of animals faced ENE or released by removal of a covering container (Fig. 6C, D, respectively) are random ($r < 0.20$) and show no relation to the true homeward direction, SSE. These results demonstrate that under the conditions of these experiments the animals have no preferred direction in relation to the way they were traveling when collected or in relation to the direction of the home pond approximately one mile away.

DISCUSSION

Whitford and Vinegar (1966) displaced *Ambystoma maculatum* adults up to 420 ft. (*ca.* 128 m.) from a breeding pond and found they were able to return to the pond, apparently aided by a rheotactic, or perhaps olfactory, response, thereby adding support to a finding of rheotactic orientation of *A. maculatum* by Finneran (1951). Under the conditions of my experiments rheotaxis apparently plays little or no role in locating the home breeding pond.

If the four animals displaced 500 m. from their home pond had no sensory contact with that pond or known routes of travel to it, they may have used a true navigation ability (Type III orientation of Griffin, 1952; reverse displacement or bicoordinate navigation of Schmidt-Koenig, 1965) in their initial oriented headings. The life-time movements of spotted salamanders are unknown; therefore displacements to unfamiliar territory are contingent upon thorough studies before true navigation can be established.

The random headings of animals released in the arena about 1 mile away from the home pond may parallel homing studies with *Taricha rivularis* in California (Twitty, 1959, 1961). Oldham (1967) reported similar results in displacements of green frogs, *Rana clamitans*. David L. Grant (personal communication), who is continuing the studies of *Taricha* orientation, utilizes a much larger "arena" to determine headings of animals displaced large distances. Apparently *Taricha* requires some time and space to determine and maintain correct headings to the home area, but in a relatively small arena *Taricha granulosa* can utilize a sun compass to move on land in a direction that would take the animals to a home shore (Landreth and Ferguson, 1967).

Laboratory conditions may affect the performances of *A. maculatum* released in an outdoor arena. Since handling and laboratory storage of females may prevent ovulation in some unknown way (Shoop, 1967), a physiologic barrier resulting from these conditions has been demonstrated. Perhaps a similar "upset" was responsible for the results of the arena release experiments.

Since spotted salamanders leaving a breeding pond often maintain a very similar or identical track away from the pond as they took to it, the animals could conceivably run through an imprinted cue system obtained as they left the ponds as juveniles and reverse it on returns to the pond, although day-length, temperature, sun altitude, and star patterns are different. Whether they always migrate every year only in familiar territory (home range) remains unknown. Uzzell (personal communication) and I have observed other ambystomatids migrating to areas where temporary ponds were not yet formed, as is often the case with the terrestrial egg-layer of the group, *A. opacum*. I observed a population of *Ambystoma talpoideum* moving into an area where a breeding pond was previously located but road construction between breeding seasons had obliterated the previous habitat. Heusser (1960) made a similar observation of migrating toads (*Bufo bufo*). While local visual or olfactory cues may play important roles in orienting to a breeding pond, in these instances, other cues were probably operative.

Many salamanders show a decided preference for a breeding pond and return year after year. Others may adopt a new breeding pond if displaced. Until lifelong records of movements or home ranges and perceptive abilities of amphibians are known, definitive statements regarding navigation and sensory mechanisms utilized in orientation will be open to question.

Summary

1. Migrating spotted salamanders entered and departed from breeding ponds at or near the same point. This pattern was repeated for three consecutive years.

2. Animals migrating in a meadow to and from the breeding pond often traveled in a corridor 10 to 30 m. wide. Several variations from this plan were noted.

3. Spotted salamanders displaced up to 500 m. may return to the home breeding pond.

4. Migrating adults transferred from the border of one breeding pond to within 10 m. of another breeding pond did not move to the new pond as did controls.

5. Migrating adults transported from the border of one pond to the center of another failed to orient to the old pond or in the direction they were moving when captured.

6. Some adults adopted a new breeding pond when displaced.

7. Animals moved to a laboratory and then released outdoors in an unfamiliar area failed to orient to their pond or in the direction they were moving when originally collected. Handling and laboratory conditions may have altered normal behavior.

8. Since lifelong records of salamander movements are lacking, certainty of navigation ability may be questioned.

9. Sensory bases for orientation remain poorly known.

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